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Phenotypic Noise and the Cost of Complexity

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• Background

Theory predicts that **phenotypic noise** is positively selected under **directional selection** because it increases the mean fitness value, and counter-selected under **stabilizing selection (1)**.

It has been suggested that under directional selection, the fitness gain provided by phenotypic noise also **promotes adaptive evolution (2)**, while the link is unclear.

Evolution on multiple phenotypic characters suffers from the **cost of complexity (3)**.

The impact of phenotypic noise in multidimensional phenotypes is less understood.

• Methods

We used a quantitative model to study the adaptive evolution of organisms with multiple phenotypic traits under selection and evolvable phenotypic noise **(4)** in a generalized fitness landscape.

• Results

Phenotypic noise promotes adaptative evolution under directional and/or stabilizing selection if the **logarithmic fitness plateaus**.

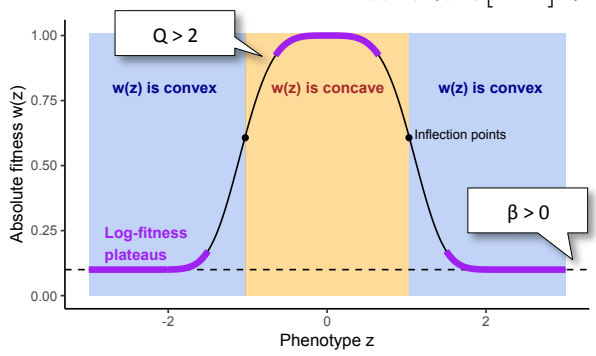
For multiple phenotypic characters under selection, the phenotypic noise evolves to a one- dimensional noise aligned with the direction of the fitness optimum.

• Conclusion

Phenotypic noise can **decrease the cost of complexity** and **promotes adaptive evolution in flat regions of the fitness landscape**.

1. Phenotypic noise effect on fitness depends on the shape of the fitness landcape (single character)

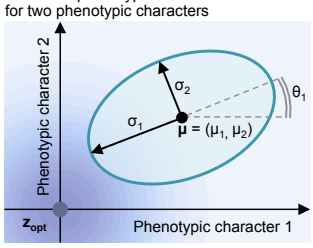
Generalized fitness function: $w(z) = (1-\beta)\exp\left[-\alpha z^{Q}\right] + \beta$ **(5)**



	Stabilizing selection (close to the fitness optimum)		Directional selection (far from the fitness optimum)	
Parameters	**Q = 2**	**Q > 2**	**β = 0**	**β > 0**
Shape of the absolute fitness function	**concave (curvature < 0)**	**concave (curvature < 0)**	**convex (curvature > 0)**	**convex (curvature > 0)**
Shape of the log-fitness function	does not plateau	**plateaus**	does not plateau	**plateaus**
Does noise increase mean absolute fitness?	No	No	Yes	Yes
Does noise promote evolution?	No	Yes	No	Yes

2. A model for phenotypic noise evolution

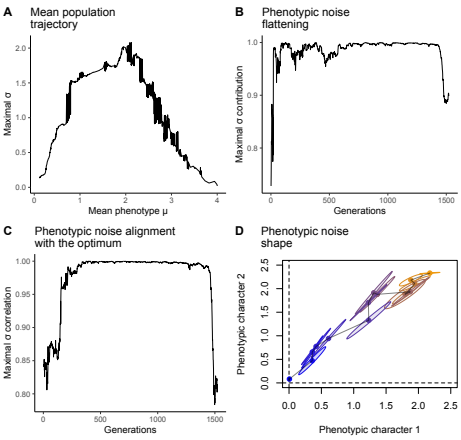
Evolvable phenotypic noise for two phenotypic characters



Multi-dimensional phenotypic noise is built from the mutable genotype {μ, σ, Θ}:

- Mean phenotype **μ** (mutable),
- Variances **σ²** (mutable),
- Rotation angles **Θ** (mutable),
- Covariance **Σ** built from **σ²** and **Θ**.
- Phenotype $z \sim N_n(\boldsymbol{\mu}, \boldsymbol{\Sigma})$

3. Phenotypic noise dimensionality reduction

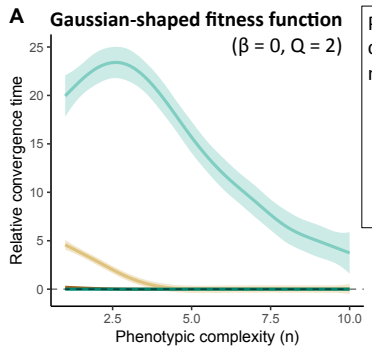


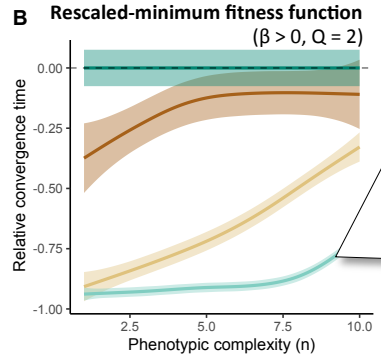
For multiple phenotypic characters under directional selection, we demonstrate that the best phenotypic noise configuration is **aligned and fully correlated with the direction of the fitness optimum**.

Example:
Simulation for two phenotypic characters:

- Initial distance: 4 units,
- Population size: 1,000,
- Mutation rate: 1^{e}-3,
- mutation size: 0.01.

4. Phenotypic noise promotes adaptive evolution and decreases the cost of complexity





Under directional selection, phenotypic noise dimensionality reduction and alignment with fitness optimum promotes the fixation of beneficial mutations and **strongly decreases the cost of complexity**.

Experimental results on Yeast (Metzger et al. 2015) suggest that phenotypic noise evolves faster than mean phenotype.

- **Phenotypic noise:** variability in phenotypes of isogenic organisms in constant environment, aka developmental noise, phenotypic heterogeneity, cellular noise, biological noise, intra-genotypic variability, ...
- **Directional selection:** selection far from fitness optimum characterized by a convex (positive second derivative) fitness landscape.
- **Stabilizing selection:** selection close to fitness optimum characterized by a concave fitness landscape.
- **Adaptive evolution:** capacity of increasing mean population fitness as measured by the rate of increase of the log-fitness with respect to the mean phenotype.
- **Cost of complexity:** Reduction of the fraction of beneficial mutations when the number of phenotypic characters under selection increases.

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